

# **Nutrients and primary production along the eastern Aleutian Island Archipelago**

**CALVIN W. MORDY,<sup>1,\*</sup> PHYLLIS J. STABENO,<sup>2</sup> CAROL LADD,<sup>1</sup> STEPHAN ZEEMAN,<sup>3</sup> DAVID P. WISEGARVER,<sup>2</sup> SIGRID A. SALO<sup>2</sup> AND GEORGE L. HUNT JR.<sup>4</sup>**

<sup>1</sup> *Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98195-4235*

<sup>2</sup> *Pacific Marine Environmental Laboratory, NOAA, Seattle, WA, 98115-6349*

<sup>3</sup> *University of New England, 11 Hills Beach Road, Biddeford, ME 0400*

<sup>4</sup> *Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525*

\*Correspondence:

e-mail: Calvin.W.Mordy@noaa.gov

phone: (206) 526-6870

fax: (206) 526-6744

**Running title:** Nutrients and primary production in the Aleutians

## **ABSTRACT**

The distribution of nutrients (nitrate, phosphate and silicic acid), chlorophyll and primary productivity were examined in the central and eastern Aleutian Archipelago. The data were collected from moorings (temperature, salinity, nitrate and currents) and two hydrographic research cruises (June 2001 and May–June 2002). During the hydrographic cruises, salinity, temperature, nutrients, chlorophyll and primary production were measured in and around the eastern and central Aleutian Passes. The net nutrient transport through the passes was northward, and was relatively low in the eastern passes compared to the central passes. In the shallow eastern passes, the source water from the Pacific was the nutrient-poor Alaska Coastal Current, while in the deeper central passes, it was the nutrient-rich Alaska Stream. Within the passes, vigorous tidal mixing resulted in enriched surface concentrations, especially in the central passes. Hydrographic chlorophyll sections and satellite composites from summer indicate high chlorophyll east of Samalga Pass and very low chlorophyll between Samalga and Segum Passes. Production was relatively low across the study area, except at the northern end of Segum Pass and in the vicinity of the shelf edge in the southeastern Bering Sea. Production and chlorophyll concentrations were lowest in the deep passes. These results suggest that, within the passes, deep mixing inhibits new production, but substantial blooms may occur downstream of the passes subsequent to stratification.

## **KEY WORDS**

Aleutian, chlorophyll, moorings, nitrate, nutrient, primary production

## INTRODUCTION

Interspersed in the Aleutian Island Archipelago are passes that permit interchange and transport of heat, salts and nutrients between the Pacific Ocean and the Bering Sea. In addition, within these passes, deep vertical mixing occurs that introduces nutrients into the euphotic zone. Two recent studies that examined the interchange, transport and mixing in the passes between Unimak Pass and Tanaga Pass are summarized below (Ladd *et al.*, 2004; Stabeno *et al.*, 2004).

While mean transport through the passes is northward, this transport is not uniform, but varies in intensity and direction both spatially across the passes (Favorite, 1974; Reed and Stabeno, 1994), and temporally on tidal, seasonal and interannual time-scales (Reed, 1990). For example, hydrographic sections across Amchitka Pass showed northward flow on the eastern side of the pass and southward flow on the western side of the pass (Reed and Stabeno, 1994). Such bi-directional flow has long been observed (Veniaminov, 1840, as translated by Roden, 1995) and may be typical for passes wider than an internal Rossby radius. Drifter tracks also have shown bi-directional flow, and indicated clockwise circulation around some of the islands (forced by the diurnal tide, Reed and Stabeno, 1994). Flow into the Bering Sea is incorporated into the northeastward flowing Aleutian North Slope Current (ANSC) that continues to flow along the northern side of the archipelago to the shelf break in the southeastern Bering Sea (Stabeno and Reed, submitted).

In the eastern passes (passes east of Samalga Pass as defined by Ladd *et al.*, 2004), northward transport is comprised predominantly of waters from the Alaskan Coastal Current (ACC), while transport in the central passes (west of Samalga and east of

Amchitka) is comprised predominantly of waters from the Alaskan Stream. The eastern, more coastal passes (e.g. Unimak, Akutan, and Umnak) are shallow and narrow, and occur on a relatively wide shelf with sill depths of <60 m. The central, more oceanic passes are deeper and wider with sill depths ranging from ca. 160–450 m along a shelf that narrows to the west. These differences in shelf width, sill depths and source waters may be the basis of an ecological boundary between the eastern and central passes.

Samalga Pass represents a transition between the eastern and central passes. It is the farthest west that waters of the ACC have been observed, and it represents a clear ecological boundary with the species distributions of seabirds and zooplankton partitioning at Samalga Pass, as well as the diets of Steller sea lions (*Eumetopias jubatus*) (Sinclair and Zeppelin, 2002; Coyle, 2004; Jahncke *et al.*, 2004). It is unclear how this ecological boundary is related to changes in nutrient content and/or primary production; i.e. bottom-up forcing. Historical data are sparse, and there have been no systematic examinations of nutrients and phytoplankton production in the Aleutian Passes.

To improve our understanding of the distribution of nutrients and primary production in the passes, and the potential impact these factors might have on higher trophic levels, we undertook a 2-year study of the distribution of nutrients and production in the eastern and central passes (east of 180°) of the Aleutian Island Archipelago. Data were collected from moorings, hydrographic surveys and primary production incubations in 2001 and 2002 (Fig. 1). Our findings present a broad view of production in the eastern and central Aleutian Archipelago, and are presented within the framework of the hypothesis that there is a significant ecological boundary at Samalga Pass.



## METHODS

### *Hydrography*

Hydrographic transects through and across the eastern and central Aleutian Passes were undertaken on the R/V *Alpha Helix* in June 2001 and May–June 2002. During June 2001, 117 CTD (conductivity, temperature, fluorescence and depth) casts were taken in four along-pass sections (Unimak, Akutan, Amukta and Seguam Passes) and two across-pass sections (Seguam and Amukta). During May–June 2002, data were collected from 164 CTD casts. The 2002 expedition revisited the passes explored in 2001, and made new observations at three other passes (Umnak, Samalga and Tanaga). Initial transects in 2002 were across Akutan and Unimak Passes on May 22 and 25 respectively (nearly a month earlier than in 2001). Then the expedition shifted to Tanaga Pass in the west, and worked eastward ending with sparse re-occupations of Unimak and Akutan Passes on 19 June. This approach allowed a comparison of late spring and early summer production in the two eastern passes. CTD casts were taken with a Seabird SBE-911 Plus system. Salinity calibration samples were taken on all casts and analyzed on a laboratory salinometer.

### *Nutrients*

Water samples for dissolved inorganic nutrients ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{HPO}_4^{2-}$ , and  $\text{H}_2\text{SiO}_4^{2-}$ ) were collected using 5-liter Niskin bottles. Samples were syringe-filtered using 0.45  $\mu\text{m}$  cellulose acetate membranes, and the filtrate was collected in 30 ml acid-washed high-density polyethylene bottles after three rinses. Samples were frozen at  $-20^\circ\text{C}$  with care to leave appropriate head space and to freeze upright (Dore *et al.*, 1996). The majority of

samples were analyzed at PMEL within 8 months, but some samples were analyzed 11 months after collection. Samples were thawed in a cool water bath and immediately analyzed. Phosphate concentrations were determined using a Technicon AutoAnalyzer II; silicic acid, nitrate and nitrite concentrations were determined using components from Alpkem and Perstorp instrumentation. Analytical methods were from Armstrong *et al.* (1967) and Atlas *et al.* (1971). Standardization and analysis procedures specified by Gordon *et al.* (1993) were closely followed including calibration of labware, preparation of primary and secondary standards, and corrections for blanks and refractive index. Nitrate and phosphate were accurate to <2% full scale (<1  $\mu\text{M}$  nitrate and <0.06  $\mu\text{M}$  phosphate). Due to the potential for polymerization of silicic acid in frozen samples (Macdonald *et al.*, 1986), a second analysis was performed after refrigeration for several days. Replicate silicic acid measurements were, on average, within 0.3  $\mu\text{M}$ . This result was consistent with the lab analysis of Macdonald *et al.* (1986) that at low silicic acid:salinity ratios and with sufficient thawing, no loss of reactive silicic acid was observed.

#### *Primary Productivity, Chlorophyll-a, and SeaWiFS Imagery*

Water for photosynthesis vs. irradiance (P-I) incubations was collected at two depths, near the surface and from the chlorophyll maximum (or from below the thermocline if no maximum was found). These sample depths seem to lead to more accurate estimates than a sample from one depth (Heilmann *et al.*, 1994). All water samples were obtained with 5- or 10-liter Niskin bottles mounted on the CTD rosette, and primary production measurements were made at stations occupied between 10:00 and 14:00 hrs local time.

Primary productivity rates were estimated using  $^{14}\text{C}$ -labeled bicarbonate (5–10  $\mu\text{Curies}$ ) in triplicate incubations (300 ml polycarbonate bottles) at eight light intensities (fluorescent tubes) between 0 and 600  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$  in an artificial light incubator maintained at sea-surface temperature (Zeeman, 1985; Zeeman and Jensen, 1990a; Lohrenz, 1993). Other investigators used many more light intensities to determine the P-I parameters, but in the tradeoff used much smaller samples. Experiments comparing bottles from 25 ml to 2 liters have demonstrated that higher photosynthetic rates are obtained using larger bottles, presumably because the enclosure effects of smaller bottles impair the phytoplankton in some manner (S.I. Zeeman, unpublished). The 300 ml samples also have the advantage of being comparable to many previous field studies which have used BOD bottles. Light intensities of 200–300  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$  have been found to be saturating ( $P_{\text{max}}$ ) in the Bering Sea, and photoinhibition has also been observed in some samples using these methods (Zeeman and Jensen, 1990a; 1990b).

The samples were incubated for 1 hr and then filtered (0.45  $\mu\text{m}$  pore size). Residual carbonate was driven off by addition of 0.5 ml of 1N HCl to the 8 ml scintillation vial containing the filter. After one hour, Ecolume® fluor was added and the vials counted by liquid scintillation. Primary production rates were then calculated using light-dark counts, and normalized to chlorophyll-*a* concentrations (Evans *et al.*, 1987). Photosynthesis vs. irradiance (P-I) data were fit to a hyperbolic tangent function with and without photoinhibition using non-linear least squares regression techniques (Jassby and Platt, 1976; Platt *et al.*, 1980). The best-fit model was determined by examining the sum of squares obtained from the regressions (Systat Inc.).

Daily in situ production was calculated from the following inputs into a numerical integration model (Zeeman, 1992; Zeeman and Jensen, 1990a; 1990b; Whitledge *et al.*, 1988): chlorophyll-specific P-I rates from the incubator, continuous recordings of 10-minute average surface irradiance (Biospherical QCP-2100 sensor), in situ measurements of irradiance from CTD profiles (Biospherical QSP-2100 sensor), and fluorometer profiles (Wetlabs fluorometer) converted to chlorophyll by standardization with extracted samples. A study of production models shows that numerical integration as done here provides the best estimates of production because continuous measurements of light were made (Zimmerman *et al.*, 1994). Extinction coefficients were calculated from subsurface PAR measurements averaged at 1 m depth intervals on the CTD casts. Extracted chlorophyll was determined on a Turner Model TD-700 fluorometer after rapid freezing of samples on GF/F filters followed by a 24-hour acetone extraction in the dark at  $-10^{\circ}\text{C}$  (Evans *et al.*, 1987).

To create the chlorophyll composite, we ordered level 1A SeaWiFS files from the Goddard DAAC and processed them with SeaWiFS Data Analysis System (SeaDAS) to obtain mapped files of OC4 chlorophyll. A composite was created from all files within thirty-day windows as the region was too cloudy to allow for shorter time limits.

### *Moorings*

Temperature, salinity, current and nitrate sensors were mounted on taut-wire subsurface moorings within 15 m of the bottom in the northern Gulf of Alaska and in southern Segum Pass (Fig. 1). The moorings were deployed in May, and recovered and redeployed in September of each year (Stabeno *et al.*, 2004). The nitrate sensors were

only deployed in the spring, and only functioned for 1 month in 2001 and 16 days in 2002. Moorings in the Gulf of Alaska (GoA) were deployed at the head of Amatuli Trough (59.109°N, 150.082°W) in 2002 (161 m), at the mouth of Amatuli Trough (59.043°N, 148.693°W) in 2001 (185 m) and 2002 (192 m) and in Chiniak Trough (57.516°N, 151.442°W) in 2002 (123 m). The Sequam Pass moorings were deployed south of Sequam Island (52.134°N, 172.420°W) in 2001 and 2002 (151 m). The moorings included an RDI 300 kHz Workhorse Sentinel Acoustic Doppler Current Profiler (ADCP), SeaBird Instruments MicroCat temperature and salinity sensors, and EnviroTech nitrate monitors (model NAS-2E). Internal calibration factors for the MicroCat were verified by the manufacturer prior to deployment and after recovery.

The NAS-2E is a syringe-driven (discrete) analyzer that measures nitrate in a similar fashion to our benchtop autoanalyzer. Nitrate is reduced to nitrite in a cadmium column, formed into a red azo dye by complexing nitrite with sulfanilamide and N-1-naphthylethylenediamine, and the complexed nitrite is measured colorometrically. Because the instrument did not make separate measurements of nitrite, units reported for the moored instrument are  $\mu\text{M}$  nitrate+nitrite (N+N). Seawater samples and calibration standards were analyzed at 6-hr intervals. Blanks were analyzed prior to each measurement, and consisted of measuring the absorbance of a standard or sample without reagents.

Calibration standards for the NAS-2E were prepared according to guidelines provided by Gordon *et al.* (1993). Working standards were made in low-nutrient seawater (LNSW) with a known nitrate concentration and stabilized by pasteurization at 80°C for 6 hours according to Aminot and K  rouel (1998). To verify stability, standards

were analyzed before mooring deployment and again after mooring recovery. The moored standards were found to be within 0.2  $\mu\text{M}$  nitrate.

## RESULTS

In 2001 and 2002, hydrographic-, chlorophyll- and nutrient-sections and primary productivity measurements were made through two eastern Aleutian Passes (Unimak Pass and Akutan Pass) and two central Aleutian Passes (Amukta Pass and Seguam Pass). In 2002, additional observations were made through Samalga and Tanaga Passes. Most of these studies were conducted in early summer with the expectation that these results represent post-spring bloom conditions. In 2002, the eastern passes were explored in May, perhaps near the end of the spring bloom, and again about 2 weeks later in what was considered to be a post-bloom environment. Satellite imagery was too sparse (due to frequent cloud cover) to determine the exact timing of the spring bloom.

### *Nutrient Distributions*

Nutrient-sections through the passes from the North Pacific to the Bering Sea are shown in Figs. 2–4. Nutrient concentrations through the eastern passes (Unimak and Akutan) were lower than in the central passes (Amukta, Seguam, Samalga and Tanaga). For example, in both years, surface nitrate in Unimak and Akutan Pass were  $<15 \mu\text{M}$ , whereas concentrations within Seguam Pass were  $25\text{--}35 \mu\text{M}$  (Fig. 2). Likewise, in 2001, surface silicic acid concentration increased from  $<30 \mu\text{M}$  in Unimak and Akutan Pass to  $40\text{--}70 \mu\text{M}$  in Seguam Pass (Fig. 4). However, there were instances in the southern portion of the central passes where surface waters were nutrient-poor (e.g. nitrate and silicic acid in Amukta Pass, 2001, and nitrate in Seguam Pass, 2002). Moreover, in the 2001 Amukta Pass section, silicic acid-poor surface water extended north to the sill (Fig. 4). But even in these instances, beneath the surface the nutrient content of the Pacific end-member was higher for the central passes compared to the eastern passes at

corresponding depths.

In Seguam Pass, nutrient concentrations were higher in the interior of the pass than at the northern or southern extreme, suggesting vigorous mixing within the pass. In 2001, the water column over the sill of Sequam Pass was completely mixed; and, in 2002, surface nutrient concentrations in this pass were the highest observed during the study.

In some of the passes, and especially in the eastern passes, higher-nutrient water from the ANSC was observed intruding at depth onto the northern flank of the pass, and contributing to higher surface nutrients over the northern flank. For example, in Amukta Pass, the water column was never completely mixed and, in the upper 100 m, concentrations of all nutrients generally increased from the Pacific northward into the Bering Sea.

In the 2001 Unimak Pass transect, the highest surface concentrations of nutrients were observed within the pass, but in 2002, nutrient concentrations were highest at the northern end of the pass. This difference could have been caused by a combination of tidal currents and low-frequency currents. However, because the northern portion of the 2001 and 2002 sections through Unimak Pass were both sampled during a southward tidal flow, the second mechanism is more likely. Low frequency currents can transport different water types along the ANSC which may be incorporated into the passes. For example, mixing of Bering Sea water with North Pacific water occurs during each tidal cycle in the central and northern portion of Unimak Pass (Stabeno *et al.*, 2002).

In the central passes, nitrate and phosphate concentrations were significantly higher in 2002 compared to 2001. (Nitrate was about 3–5  $\mu\text{M}$  higher and phosphate was about 0.2  $\mu\text{M}$  higher). This interannual variability may have originated from differences



in primary production and nutrient drawdown, from sampling during different phases of the tides, or from variability in source waters of the Alaskan Stream. In the eastern passes, while there were some examples of interannual variability (e.g. the northern end of Unimak Pass was more nutrient-rich in 2002), most of these differences were small and the nutrient distributions were similar in both years.

Nutrient-salinity diagrams were generated using hydrographic data from 2002 and 2001 (Fig. 5). (The nitrate-phosphate diagrams for each respective year are also shown, Fig. 5g, 5h.) These plots incorporate all of the hydrographic data, with the more shallow stations east of Samalga Pass shown in gray, and the deeper stations from Samalga Pass westward shown in black. The nutrient-salinity relationships are non-linear with the nitrate-salinity (Fig. 5a, 5b) and phosphate-salinity (Fig. 5c, 5d) relationships tailing off at the nutrient maximum, and a concave relationship between silicic acid and salinity (Fig. 5e, 5f) (the different shapes result from different mechanisms of remineralization). In both years, there was a clear transition in the nutrient-salinity relationships at Samalga Pass. East of Samalga Pass, salinities were generally <33 psu and nutrient levels were relatively low with considerable scatter. From Samalga Pass westward, salinities were greater than 32.5 psu and the nutrient concentrations were much higher.

The large amount of variability in the nutrient-salinity diagrams could have resulted from the freezing of nutrient samples, from freshening events, or from phytoplankton production and concomitant nutrient drawdown. While freezing of samples can reduce precision (see discussion by Dore *et al.*, 1996), there was little variability in the nitrate-phosphate relationship (Figs. 5g and 5h) indicating that the nutrient analysis was relatively precise. Because the ACC has a strong fresh water core

and dominates flow in the passes east of Samalga, it is unlikely that salinity was conservative east of Samalga Pass. Indeed, the influence of this fresher coastal flow was evident in the eastern passes in the occurrence of very low salinity water. Of greatest interest to this study was the drawdown of nutrients from primary production.

From the nutrient-salinity diagrams, it was evident that nutrient drawdown was substantial in 2001 relative to 2002. In 2001, data from the eastern passes was quite scattered, suggesting an unknown combination of freshening and nutrient drawdown via primary production. In the central passes, substantial drawdown was observed for nitrate, phosphate and silicic acid, and was observed even in water below 100 m.

In 2002, some of the depleted nutrient data at salinities 32.6–32.7 psu (Figs. 5b and 5d) were from surface samples at the southern extreme of Samalga and Amukta Pass. But most of the depleted samples (data at salinities of 32.57 and 33.16 psu) were from the upper 50 m in Seguam Pass. Not only were these samples depleted in nutrients, but the nitrate:phosphate ratios were higher compared to the remaining data (Fig. 5h, these points were outside the 99% prediction interval for the linear regression of data from the central passes). Removal rates of nitrate and phosphate are known to be species dependent (Arrigo *et al.*, 1999). Such nutrient anomalies (higher nitrate:phosphate ratios) have been observed during *Fragilariopsis kerguelensis* blooms in the Southern Ocean, a species known to vary its uptake ratio of nitrate:phosphate depending on the ambient iron concentration (De Baar *et al.*, 1997). Likewise in the North Pacific, nutrient uptake rates of diatoms can vary depending on ambient iron concentrations (Firme *et al.*, 2003; Franck *et al.*, 2004), and evidence suggests that iron may be limiting over parts of the Gulf of Alaska (GoA) shelf in summer (S. Strom, pers. comm).

### *Chlorophyll and Primary Production*

Sections of chlorophyll-*a* (Fig. 6) clearly show that phytoplankton abundance was much higher in Unimak and Akutan Pass than in the central passes. In the eastern passes, the distribution of chlorophyll was quite patchy with low concentrations in the center and the highest concentrations to the north. In the central passes, chlorophyll concentrations were very low except for a sub-surface maximum at the southern end of Amukta Pass in 2001, and the very large sub-surface bloom in Seguam Pass in 2002. Chlorophyll concentrations were generally lower in regions of strong mixing (e.g. Unimak Pass, 2002 at 40 km), as evidenced by the density distributions and mooring data (Stabeno *et al.*, 2002; Ladd *et al.*, 2004).

To augment the hydrographic chlorophyll sections and to provide a broader view of chlorophyll distributions, a 6-year (1998–2003) composite of summer SeaWiFS images was developed (Fig. 7a). (Individual satellite images were sparse due to frequent cloud cover). The composite shows that, in summer, the accumulation of chlorophyll was generally low within the passes, and was especially low between Samalga Pass and Seguam Pass. There was a moderate chlorophyll front across the northern end of Seguam Pass, and one of the most intense chlorophyll accumulations was observed at the northern end of Akutan Pass, representing the southern end of the shelf-edge bloom in the Bering Sea (Springer *et al.*, 1996). These were consistent features taken from numerous images (Fig. 7b), and were in agreement with the hydrographic sections (Fig. 6). In contrast, the composite indicates a region of high chlorophyll north of Tanaga Pass; but this feature was the product of only a few images (Fig. 7b), and the hydrographic section in 2002 showed very low chlorophyll content there.

Productivity measurements were designed to examine for longitudinal trends, for latitudinal trends through the passes, and for variability in production between 2001 and 2002. In 2001, primary production was measured at the northern and southern extreme of two eastern passes and two central passes (Fig. 8a). In 2002, primary production was measured to the north and south of seven passes, but also included measurements in the center of the passes where we expected the water to be well mixed (Fig. 8b). In addition, production in the eastern passes was measured in late May (Fig. 8b inset) and about 2 weeks later in early June. A table of production rates and PI parameters for each production station are shown in the appendix.

In 2001, production was considerably higher in the eastern passes than in the central passes (Table 1). Production was especially high at the northern end of Unimak and Akutan Passes concomitant with regions of high chlorophyll content. In the central passes, production was low. Opposite trends of production were observed at Amukta and at Seguam Passes as the highest production was observed to the south at Amukta Pass in a region of depleted nitrate and silicic acid.

In 2002, although average integrated primary production was significantly higher in May than in June (Table 1), instances of relatively low production ( $<500 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) were observed during both periods. The highest production rate ( $6,570 \pm 850 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) was observed at the northern end of Akutan Pass in May 2002 in an intense chlorophyll patch. Primary production in June was low ( $<600 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) with a few exceptions. Slightly higher production was observed in the eastern passes, e.g. at the northern and southern end of Akutan Pass, and the northern end of Unimak Pass. However, there was very little production across Umnak Pass. Along the central passes,

substantial production was only observed in the center and at the northern end of Seguam Pass.

Comparing production from the 2 years we find that in June 2001, integrated production in the eastern passes was intense and greater than average production observed in May 2002 (Table 1); i.e., production in June 2001 was more spring-like. The interannual variability was more evident when comparing the June data sets from the eastern passes. Averaged daily production in 2001 was nearly tenfold that in 2002, a result supported by the extensive nutrient drawdown observed in 2001 (shown above).

Productivity experiments also focused on whether there was higher production north or south of the Aleutian Passes. On the whole, statistical analysis could detect no differences, with several specific exceptions. In both years, production was higher at the northern end of Seguam Pass, and the highest production rates were observed at the northern end of Akutan Pass (June 2001 and May 2002). We also examined the longitudinal distribution of integrated primary production (Fig. 9). While there was high production at the northern end of Akutan and Unimak Passes in 2001 and May 2002, no significant trend was observed. In June 2002, the highest production was observed in Seguam Pass rather than in the eastern passes.

### *Moorings*

The nitrate monitor on the Seguam Pass mooring only operated for short periods (Fig. 10) (one month in 2001 and 16 days in 2002). While salinity was measured hourly, N+N was measured at 6-hour intervals. Within Seguam Pass, currents were dominated by tides with speeds exceeding  $200 \text{ cm s}^{-1}$ . The dominant tidal constituent was  $K_1$  with an

amplitude of the major axis near the bottom of  $\sim 70 \text{ cm s}^{-1}$ . The amplitude of the  $M_2$  constituent ( $\sim 25 \text{ cm s}^{-1}$ ) was much less (Stabeno *et al.*, 2004).

Because the tides were dominated by a diurnal cycle, the 6-hr N+N sampling scheme usually resolved the major tidal component. The 15-day envelope in the amplitude of the tides was due to the beating of the  $M_2$  and  $K_1$  tides (Stabeno *et al.*, 2004). This 15-day tidal variability was also apparent in the N+N and salinity time series, especially from May 7–10, 2002, when low tidal amplitudes and the absence of southward flow dampened N+N and salinity variability. The variability of N+N (on tidal scales) was greatest in 2001 with an average tidal swing of  $\sim 5 \text{ } \mu\text{M}$  N+N compared with  $\sim 2 \text{ } \mu\text{M}$  in 2002.

In 2001, while the NAS-2E was operating, several hydrographic stations were occupied 18–27 km west of the mooring. To compare these data sets, the nearest hydrographic data were linearly interpolated to the mooring depth, and mooring data were linearly interpolated to the cast time. On June 10, the hydrographic N+N and salinity were  $6 \text{ } \mu\text{M}$  and 0.21 psu higher respectively than the moored data, while on June 11, these parameters were  $8 \text{ } \mu\text{M}$  and 0.21 psu lower than the moored data. If the tidal cycle between the mooring location and the hydrographic casts were shifted by 3.3 hours, then the mooring and discrete N+N agree to within  $1.0 \text{ } \mu\text{M}$ . These results suggest that discrepancies between the moored and hydrographic nitrate data were not operational, but the result of spatial and temporal variability in the nutrient and salinity fields, not too surprising as the distance between these sampling platforms was greater than a Rossby radius. The discrete samples do help to verify the dynamic range of N+N observed at the moorings.

At the mooring site (south of the sill), salinity and N+N concentrations varied on semi-diurnal frequencies, but the tidal velocity varied diurnally. This inconsistency was explained by jointly examining tidal flows north and south of the pass. North of the pass, the tidal velocity and temperature varied semi-diurnally (see Fig. 6 in Staben *et al.*, 2004). Therefore, there were periods when the tidal currents to the north and south of the pass were in phase, and periods when these flows were opposed.

When the tidal flows were in phase and northward, recirculation around the islands was minimized, and water over the mooring was representative of the deep Pacific source water. When tides were out of phase, water exiting Amukta Pass to the south were forced westward by the Alaskan Stream, and incorporated into the northward diurnal tidal current through Seguam Pass. This water was well mixed and representative of the lower nutrient and salinity water that was observed at the mooring near the end of the diurnal tidal cycle.

As shown in Fig. 11, the slope of the relationship of N+N against salinity from the Seguam Pass moored analyzer was significantly lower in 2002 than in 2001 ( $F = 100.1$ ,  $P < 0.0001$ ). Although the dynamic range of salinity was similar in 2001 and 2002 (33.33 to 33.71 psu, Figs. 11a and 11b), the dynamic range of N+N was smaller in 2002 by more than 6  $\mu\text{M}$ . (The range of N+N was 23.7–40.4  $\mu\text{M}$  in 2001 and 30.5–36.7  $\mu\text{M}$  in 2002.) In addition, considerably more scatter was observed in 2001 ( $R^2 = 0.77$ ) than in 2002 ( $R^2 = 0.89$ ).

The tight relationship between N+N and salinity in 2002 may be attributed in part to the sampling of only one water type, i.e., water  $< 4.1^\circ\text{C}$  compared to 2001 (Figs. 11c and 11d). The temperature-salinity diagram from the mooring showed that while the

temperature and salinity sensors sampled several water types in both years, in 2002, the nitrate monitor only sampled water  $<4.1^{\circ}\text{C}$  before failing. Ignoring 2001 data with temperatures  $>4.1^{\circ}\text{C}$ , the  $R^2$  value improved to 0.87, nearly the same as for the 2002 data, but the slopes remained significantly different ( $F = 183.3$ ,  $P < 0.0001$ ). Although the warmer water type was observed at the mooring sites, it was not observed during the hydrographic cruises in 2001 and 2002, or during the 1993 WOCE P14 cruise through Amchitka Pass (not shown).

Comparing the Seguam Pass moorings to those in the GoA (Fig. 12), we found that the N+N–salinity relationship of the mooring data was remarkably precise, especially when considering that the six mooring data sets spanned  $\sim 1000$  km from the head of the GoA to Seguam Pass. The moored nitrate monitors were all deployed at similar depths, and so likely encountered similar water types. A break in the moored N+N – salinity relationship was apparent with relatively lower N+N concentrations in water fresher than 32.5 psu. These data were from 123 m in Chiniak Trough (see Fig. 1 for location). In this trough, temperature and salinity time series from multiple depths showed deep mixing, and suggest deep penetration of nutrient-depleted, warmer, low-salinity surface water.

Except for data from the Seguam Pass mooring in 2002, the slopes of all the mooring data sets in Fig. 12 were similar. The slope for the 2002 Seguam Pass data was steeper than slopes of any of the other data sets (as shown above); however, the highest N+N values in Seguam Pass did correspond with more nutrient-rich water observed to the west on the 1993 WOCE P14 cruise through Amchitka Pass.

Different flow patterns brought different water types over the mooring. For



instance, northward flow through Amchitka Pass sometimes continues eastward along the Aleutian Islands, and at other times meanders into the basin (Stabeno *et al.*, 1999; Stabeno and Reed, submitted). The drifter trajectories also reveal complex flow in and around the islands of the archipelago (e.g. Figs. 5 and 6 in Ladd *et al.*, 2004). Thus, the source of the water flowing through the passes varies and includes water from the Pacific, recirculation of water from Amchitka Pass, water from the Bering Sea basin, and older water in the ANSC. These different flow patterns and water types may explain the warmer water type observed in the 2001 mooring data, and the steeper slope of the nitrate-salinity relationship observed in the 2002 mooring data.

#### *Nutrient Transport*

First order estimates of nutrient transport were made through several of the Aleutian Passes (Table 2) using transport values from Stabeno *et al.* (2004) and average nutrient concentrations in the Pacific source waters (depth averaged nutrient data from the sill to the southern flank). Nutrient transport through the eastern passes was very low due to the low concentration of nutrients in the source water, and shallow sill depths. In contrast, substantial transport occurs in Amukta, the deepest of the central passes. To estimate total nutrient transport through the eastern and central passes, we assumed that nitrate transport through the remaining small eastern passes was negligible, and that volume transport through Tanaga Pass and Samalga Pass was similar to transport through Seguam Pass as these passes are of similar size.

## DISCUSSION

The occurrence of higher nutrients in the oceanic central passes compared to the coastal eastern passes appears to originate from the different source waters. Upstream of the Aleutians, the ACC flows over the wide shelf of the northern GoA and is freshened by heavy precipitation and extensive runoff (Royer, 1979; 1982; Royer *et al.*, 1979; Stabeno *et al.*, 1995). Large spring blooms strip most of the nutrients from the surface water so that, by early summer, when the majority of this work was conducted, the ACC had a distinctive low salt, low nutrient signature upon reaching the Aleutians and flowing northward through the eastern passes. In contrast, the Alaskan Stream is the western boundary current of the subarctic gyre, and is the Pacific source water for northward flow through the central Aleutian Passes. The nutrient and salt signature of this water is derived from the basin and the shelf break. Surface waters in the basin represent one of the three major High Nutrient, Low Chlorophyll (HNLC) regions in the world (Martin *et al.*, 1991, Harrison *et al.*, 1999; Moore *et al.*, 2002). Here, chlorophyll concentrations in summer remain modest despite relatively high nutrient concentrations. In such HNLC regions, iron has been implicated as the constituent limiting primary production (Martin *et al.*, 1991; Suzuki *et al.*, 2002; Tsuda *et al.*, 2003).

Upwelling and deep turbulent mixing within the passes also contribute to differences in nutrient fields east and west of Samalga Pass. These processes have long been recognized as mechanisms of nutrient supply that sustain primary production in summer (Barnes and Thompson, 1938; Kelly and Hood, 1971; Hood and Kelly, 1976; Swift and Aagaard, 1976; Sambrotto and Lorenzen, 1987). We observed deep mixing in most of the passes, and at times the water column was completely mixed.

The eastern passes were so shallow that nutrient concentrations at the sill depth were relatively low; i.e. there was just too little nutrient content in the ACC to substantially enrich surface concentrations via deep mixing (relative to the central passes). For example, surface nitrate concentrations on the southern side of Unimak and Akutan Passes (ACC water) were generally  $<5 \mu\text{M}$ . On the northern side of these passes, deep mixing of intruding water from the Aleutian North Slope Current provided higher concentrations of nutrients to the surface with nitrate reaching  $10\text{--}15 \mu\text{M}$ . While these nutrient levels were lower than in the central passes, nutrient pumping at the northern end of the eastern passes was sufficient to support substantial blooms in 2001 and in May 2002.

West of Samalga Pass, sill depths were below the nutricline ( $\sim 100\text{--}150 \text{ m}$ ); consequently, euphotic-zone nutrients were enriched significantly via deep mixing. For example, surface concentrations in Tanaga and Seguam Passes (sill depths of about 240 m and 170 m, respectively) were  $>25 \mu\text{M}$  nitrate. In Sequam Pass, water was mixed to the bottom in 2001, and mixing at the mooring site (south of the sill) was more complete during a southern tidal flow (Stabeno *et al.*, 2004).

We hypothesize that the difference in nutrient concentrations between the eastern and central passes fluctuates seasonally, and that this difference is maximized in summer. In summer, freshening and solar heating stratify waters of the ACC and promote production and nutrient drawdown. Hence, the source water of the eastern passes is nutrient-poor in summer. In winter, this difference is minimized as deep winter mixing entrains nutrients into the ACC as it moves westward into the Aleutians.

Although deep tidal mixing may act as a nutrient pump for the surface, mixing

below the critical depth hinders the development of phytoplankton blooms (Sverdrup, 1953; Smetacek and Passow, 1990; Nelson and Smith, 1991; Platt *et al.* 1991; Huisman *et al.*, 1999). For example, McRoy *et al.* (1972) found that production in Unimak Pass was lower to the south and within the pass relative to the northern flanks of the pass, i.e. production was lower in regions of strong mixing.

In this study, we observed massive chlorophyll blooms ( $10\text{--}20\text{ mg m}^{-3}$ ) east of Samalga Pass, and satellite imagery suggests that these blooms were persistent through the summer. While chlorophyll accumulations were highest at the northern and southern ends of the eastern passes, in the center of these passes, deep tidal mixing limited the accumulation of chlorophyll.

In contrast, there was a vast region from Samalga Pass to Seguam Pass in which chlorophyll concentrations were extraordinarily low (Fig. 7). In this area, the passes were deep, wide and short, and were separated by relatively small islands. Due to the length (shorter than the tidal excursion) and width (greater than an internal Rossby radius) of these passes, bi-directional flow and circulation around these islands were most certainly common (Stabeno *et al.*, 2004). We speculate that these waters flowed repeatedly through the central passes and were therefore continually mixed. Hence, we suggest that from Samalga Pass to Seguam Pass, phytoplankton were continually mixed below the critical depth, thereby limiting chlorophyll accumulation and primary production in this region.

From Seguam Pass to Tanaga Pass, larger islands and narrower passes impede bi-directional flow. As a result, waters north of Seguam Pass were moderately stratified and supported large chlorophyll accumulations.

Like McRoy *et al.* (1972), we found the highest production to be north of Akutan in the vicinity of an intense chlorophyll bloom. However, in the eastern passes, our averaged daily June production rates were 2 to 17 times higher than those reported by McRoy *et al.* Likewise in the central passes, our productivity rates were 2 to 3 times those of McRoy *et al.* The nature of this discrepancy is unclear, but may be due in part from McRoy *et al.* only integrating to the 25% light depth.

In a recent overview of production estimates in the Aleutians and Bering Sea, Springer *et al.* (1996) provided very general annual production rates of  $150\text{--}200 \text{ g C m}^{-2} \text{ yr}^{-1}$  across the entire Aleutian Island Archipelago. Assuming a 4-month growing season (Hansel *et al.*, 1993), averaged daily production rates for Springer *et al.* (1996) were  $1230\text{--}1640 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; results similar to the average production found in this study ( $1510 \pm 120 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). However, we also found that primary production rates varied widely ( $40 \pm 30$  to  $6810 \pm 920 \text{ mg C m}^{-2} \text{ d}^{-1}$ ), spanning far beyond the generalized rates given by Springer *et al.* (1996).

While measurements of phytoplankton production provide a relatively instantaneous measurement under prevailing (patchy) conditions, the depletion of inorganic nutrients integrates production over time and space, and provides some measure of the productive history of the water. The drawdown of nutrients was used to help verify several major conclusions drawn from the sparse observations of primary production. First, nutrient drawdown and primary production were both greater in 2001 than in 2002, except in Seguam Pass where the trend in both parameters was reversed. Second, in 2002, Seguam Pass was the only central pass with substantial production and nutrient drawdown.

Ladd *et al.* (2004) describe Samalga Pass as an ecological boundary between a more coastal regime to the east, and a more oceanic regime to the west. However, we did not observe a significant longitudinal trend in the sparse primary production data. Sometimes the highest production rates were observed west of Samalga (Seguam Pass, 2002); but, at other times, the highest production rates were observed east of Samalga (in 2001 and May 2002). At the same time, low rates of production were observed at all longitudes. These observations were similar to those of McRoy *et al.* (1972). They found that despite higher surface production in Unimak Pass compared to Amukta Pass ( $5.6 \text{ mg C m}^{-3} \text{ d}^{-1}$  vs.  $31 \text{ mg C m}^{-3} \text{ d}^{-1}$ ), integrated productivity was similar east and west of Samalga Pass.

Another significant observation of McRoy *et al.* (1972) was the extreme spatial variability of production rates in the vicinity of the passes. Likewise, in this study, it was important to examine spatial variability of the productivity measurements. Note the location of productivity stations (arrows in Fig. 6) in relation to the chlorophyll blooms. Given the extreme patchiness of chlorophyll, productivity measurements were too sparse to determine precisely longitudinal and latitudinal trends. For example, the northern productivity station in Unimak Pass in 2002 was situated in a region of low chlorophyll sandwiched between intense blooms.

Even though longitudinal trends were not evident for primary production, the longitudinal shift in chlorophyll at Samalga Pass was dramatic and was persistent over several years and throughout the summer. This, in turn, may contribute to the partitioning of zooplankton species observed at Samalga Pass (Coyle *et al.*, 2004), and the ecological boundary that occurs here.

## **SUMMARY**

Due to a difference in sill depths and source waters, nutrient transport through the eastern passes was relatively low compared with the central passes. In the shallow eastern passes, the source water in the Pacific was the nitrate depleted ACC. In the deeper central passes, the Pacific source water was the nutrient-rich Alaska Stream. Within the passes, nutrients are enriched from a combination of deep Bering Sea water intruding from the north and deep mixing, processes that occur throughout the summer. Bottom-up control of phytoplankton production in the eastern passes may be from nitrate limitation and/or deep mixing; and, in the central passes, by deep mixing. The combination of nutrient enrichment within the passes and stratification downstream of the passes provides the potential for substantial new production over the entire summer. The highest chlorophyll concentrations were observed in the eastern passes coincident with the shelf-edge bloom in the Bering Sea. In the central passes, chlorophyll concentrations were low among the small islands due to recirculation and continual deep mixing. Consequently, there was a significant longitudinal shift in chlorophyll at Samalga Pass, implying a shift in the bottom-up control of higher trophic levels. This conclusion is consistent with the hypothesis of a significant ecological boundary at Samalga Pass.

## ACKNOWLEDGEMENTS

We thank the captain and crew of the R/V *Alpha Helix* for facilitating this research. We also thank two anonymous reviewers for their valuable comments, and K. Birchfield and D. Jongeward for help in constructing the figures. Data from the WOCE P14 cruise were provided by the US WOCE office at the Scripps Institute of Oceanography. SeaWiFS level 1A data were obtained from the Goddard Earth Sciences Distributed Active Archive Center under the auspices of the National Aeronautics and Space Administration. Files were processed using SeaDAS (SeaWiFS Data Analysis System) which is maintained and distributed by the Goddard Space Flight Center. Use of this data is in accord with the SeaWiFS Research Data Use Terms and Conditions Agreement. This research was sponsored by the Cooperative Institute For Arctic Research (CIFAR), the Global Ocean Ecosystems Dynamics (GLOBEC) program, and NOAA's Steller Sea Lion Research Program, and this publication was partially funded by the Joint Institute for the Study of Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA17RJ1232. This is PMEL contribution number 2656, JISAO contribution 1040, GLOBEC contribution number 250 and Fisheries-Oceanography Coordinated Investigations (FOCI) contribution FOCI-L484.



## REFERENCES

- Aminot, A., and K  rouel, R. (1998) Pasteurization as an alternative method for preservation of nitrate and nitrite in seawater samples. *Mar. Chem.* **61**:203–208.
- Armstrong, F.A.J., Stearns, C.R., and Strickland, J.D.H. (1967) The measurement of upwelling and subsequent biological processes by means of the Technicon AutoAnalyzer and associated equipment. *Deep-Sea Res.* **14**:381–389.
- Arrigo, K.R., Robinson, D.H., Worthen, D.L., Dunbar, R.B., DiTullio, G.R., VanWoert, M., and Lizotte, M.P. (1999) Phytoplankton community structure and the drawdown of nutrients and CO<sub>2</sub> in the Southern Ocean. *Science* **283**:365–367.
- Atlas, E.L., Callaway, J.C., Tomlinson, R.D., Gordon, L.I., Barstow, L., and Park, P.K. (1971) A practical manual for the use of the Technicon AutoAnalyzer for nutrient analysis, revised. Corvallis, Oregon: Oregon State University, Technical Report 215, Reference No. 71-22.
- Barnes, C.A. and Thompson, T.G. (1938) Physical and chemical investigations in the Bering Sea and portions of the North Pacific Ocean. *Univ. Wash. Publ. Oceanogr.* **3**:35–9.
- Coyle, K.O. (2004) Zooplankton distribution, abundance and biomass relative to water masses in eastern and central Aleutian Island passes. *Fish. Oceanogr.*:this issue.

De Baar, H.J.W., Van Leeuwe, M.A., Scharek, R., Goeyens, L., Bakker, K.M.J., and Fritsche, P. (1997) Nutrient anomalies in *Fragilariopsis kerguelensis* blooms, iron deficiency and the nitrate/phosphate ratio (A. C. Redfield) of the Antarctic Ocean. *Deep-Sea Res. (II Top. Stud. Oceanogr.)* **44**:229–260.

Dore, J.E., Houlihan, T., Hebel, D.V., Tien, G., Tupas, L., and Karl, D.M. (1996) Freezing as a method of sample preservation for the analysis of dissolved inorganic nutrients in seawater. *Mar. Chem.* **53**:173–185.

Evans, C.A., O'Reilly, J.E., and Thomas, J.P. (1987) In: A handbook for the measurement of chlorophyll a and primary production. BIOMASS Scientific Series No. 8.

Favorite, F. (1974) Flow into the Bering Sea through Aleutian island passes. In: *Oceanography of the Bering Sea with emphasis on renewable resources*. D. W. Hood and E. J. Kelley (eds.), Alaska: Institute of Marine Science, University of Alaska, Fairbanks, pp. 3–37.

Firme, G.F., Rue, E.L., Weeks, D.A., Bruland, K.W., and Hutchins, D.A. (2003) Spatial and temporal variability in phytoplankton iron limitation along the California coast and consequences for Si, N and C biogeochemistry. *Global Biogeochem. Cycles* **17**:1016, doi:10.1029/2001GB001824.

Franck V.M., Bruland, K.W., Hutchins, D.A., and Brzezinski, M.A. (2004) Iron and zinc effects on silicic acid and nitrate uptake kinetics in three high-nutrient, low-chlorophyll (HNLC) regions. *Mar. Ecol. Prog. Ser.* **252**:15–33

Gordon, L.I., Jennings Jr., J.C., Ross, A.A., and Krest, J.M. (1993) A suggested protocol for continuous automated analysis of seawater nutrients (phosphate, nitrate, nitrite and silicic acid) in the WOCE Hydrographic program and the Joint Global Ocean Fluxes Study, WOCE Operations Manual, vol. 3: The Observational Programme, Section 3.2: WOCE Hydrographic Programme, Part 3.1.3: WHP Operations and Methods. WHP Office Report WHPO 91-1; WOCE Report No. 68/91. November, 1994, Revision 1, Woods Hole, Mass., USA, 52 loose-leaf pages.

Hansell, D.A., Whitledge, T.E., and Goering, J.J. (1993) Patterns of nitrate utilization and new production over the Bering-Chukchi shelf. *Cont. Shelf Res.* **13**:601–627.

Harrison, P.J., Boyd, P.W., Varela, D.E., Takeda, S., Shiomoto, A., and Odate, T. (1999) Comparison of factors controlling phytoplankton productivity in the NE and NW subarctic Pacific gyres. *Prog. Oceanogr.* **42**:205–234.

Heilmann, J.P., Richardson, K., and Ærtebjerg, G. (1994) Annual distribution and activity of phytoplankton in the Skagerrak/Kattegat frontal region. *Mar. Ecol. Prog. Ser.* **112**:213–223.

- Hood, D.W., and Kelley, J.J. (1976) Evaluation of mean vertical transports in an upwelling system by CO<sub>2</sub> measurements. *Mar. Sci. Comm.* **2**:387–411.
- Huisman, J. (1999) Population dynamics of light-limited phytoplankton: Microcosm experiments. *Ecology* **80**:202–210.
- Jahncke, J., Coyle, K.O., and Hunt Jr., G.L. (2004) Seabird distribution, abundance and diets in the eastern and central Aleutian Islands. *Fish. Oceanogr.*:this issue.
- Jassby, A.D., and Platt, T. (1976) Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.* **21**:540–547.
- Kelley, J.J., and Hood, D.W. (1971) Carbon dioxide in the Pacific Ocean and Bering Sea: Upwelling and mixing. *J. Geophys. Res.* **76**:745–752.
- Ladd, C., Hunt Jr., G.L., Mordy, C.W., Salo, S., and Stabeno, P. (2004) Marine environment of the eastern and central Aleutian Islands. *Fish. Oceanogr.*:this issue.
- Lohrenz, S.E. (1993) Estimation of primary production by the simulated in situ method. *ICES Mar. Sci. Symp.* **197**:159–171.
- MacDonald, R.W., McLaughlin, F.A., and Wong, C.S. (1986) The storage of reactive silicate samples by freezing. *Limnol. Oceanogr.* **31**:1139–1142.

Martin, J.H., Gordon, R.M., and Fitzwater, S.E. (1991) The case for iron. *Limnol. Oceanogr.* **36**:1793–1802.

McRoy, G.P., Goering, J.J., and Shiels, W.E. (1972) Studies of primary production in the eastern Bering Sea. In: *Biological oceanography of the northern North Pacific Ocean*. A.Y. Takenouti *et al.* (eds.) Tokyo: Idemitsu-shoten, pp. 199–216.

Moore, J.K., Doney, S.C., Glover, D.M., and Fung, I.Y. (2002) Iron cycling and nutrient-limitation patterns in surface waters of the World Ocean. *Deep-Sea Res. (II Top. Stud. Oceanogr.)* **49**:463–507.

Nelson, D.M., and Smith Jr., W.O. (1991) Sverdrup revisited: Critical depths, maximum chlorophyll levels, and the control of southern ocean productivity by the irradiance-mixing regime. *Limnol. Oceanogr.* **36**:1650–1661.

Platt, T., Gallegos, C.L., and Harrison, W.G. (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. Mar. Res.* **38**:687–701.

Platt, T., Bird, D.F., and Sathyendranath, S. (1991) Critical depth and marine primary production. *Proc. R. Soc. Lond. B* **246**:205–217.

Reed, R.K. (1990) A year-long observation of water exchange between the North Pacific and the Bering Sea. *Limnol. Oceanogr.* **35**:1604–1609.

Reed, R.K., and Stabeno, P.J. (1994) Flow along and across the Aleutian Ridge. *J. Mar. Res.* **52**:639–648.

Roden, G.I. (1995) Aleutian Basin of the Bering Sea: Thermocline, oxygen, nutrient, and current structure in July 1993. *J. Geophys. Res.* **100**:13,539–13,554.

Royer, T.C. (1979) On the effect of precipitation and runoff on coastal circulation in the Gulf of Alaska. *J. Phys. Oceanogr.* **9**:555–563.

Royer, T.C. (1982) Coastal fresh water discharge in the Northeast Pacific. *J. Geophys. Res.* **87**:2017–2021.

Royer, T.C., Hansen, D.V., and Pashinski, D.J. (1979) Coastal flow in the northern Gulf of Alaska as observed by dynamic topography and satellite-tracked drogued drift buoys. *J. Phys. Oceanogr.* **9**:785–801.

Sambrotto, R.N., and Lorenzen, C.J. (1987) Phytoplankton and Primary Production. In: *The Gulf of Alaska*. D. W. Hood and S. T. Zimmerman (eds.), Anchorage: NOAA, pp. 249–282.

Sinclair, E.H., and Zeppelin, T.K. (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *J. Mammal.* **83**:973–990.

Smetacek, V., and Passow, U. (1990) Spring bloom initiation and Sverdrup's critical-depth model. *Limnol. Oceanogr.* **35**:228–234.

Springer, A.M., McRoy, C.P., and Flint, M.V. (1996) The Bering Sea green belt: shelf-edge processes and ecosystem production. *Fish. Oceanogr.* **5**:205–233.

Stabeno, P.J., and Reed, R.K. (2004) Observations of the Aleutian North Slope Current, Bering Sea, 1996–2000. *Prog. Oceanogr.*: submitted.

Stabeno, P.J., Reed, R.K., and Schumacher, J.D. (1995) The Alaska Coastal Current: Continuity of transport and forcing. *J. Geophys. Res.* **100**:2477–2495.

Stabeno, P.J., Schumacher, J.D., and Ohtani, K. (1999) The physical oceanography of the Bering Sea. In *Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea*, T.R. Loughlin and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, North Pacific Marine Science Organization (PICES), 1–28.

Stabeno, P.J., Reed, R.K., and Napp, J.M. (2002) Transport through Unimak Pass Alaska. *Deep-Sea Res. (II Top. Stud. Oceanogr.)* **49**:5919–5930.

Stabeno, P.J., Kachel, D.G., Kachel, N.B., and Sullivan, M.E. (2004) Observations from moorings in the Aleutian Passes: temperature, salinity and transport. *Fish. Oceanogr.*: this issue.

Suzuki, K., Liu, H., Saino, T., Obata, H., Takano, M., Okamura, K., Sohrin, Y., and Fujishima, Y. (2002) East-west gradients in the photosynthetic potential of phytoplankton and iron concentration in the subarctic Pacific Ocean during early summer. *Limnol. Oceanogr.* **47**:1581–1594.

Sverdrup, H.U. (1953) On conditions for the vernal blooming of phytoplankton. *J. Cons. Perm. Int. Explor. Mer.* **18**:237–295.

Swift, J.H., and Aagaard, K. (1976) Upwelling near Samalga Pass. *Limnol. Oceanogr.* **21**:399–408.

Tsuda, A. *et al.* (2003) A mesoscale iron enrichment in the western subarctic Pacific induces a large centric diatom bloom. *Science* **300**:958–961.

Veniaminov, I. (1840) Notes on the Islands of the Unalaska Region. St. Petersburg: *Imperial Akad. Russia*, Vol. 1, pp. 21–25 (in Russian).



Whitledge, T.E., Bidigare, R.B., Zeeman, S.I., Sambrotto, R.N., Roscigno, P.F., Jensen, P.R., Brooks, J.M., Trees, C., and Veidt D.M. (1988) Biological measurements and related chemical features in Soviet and United States regions of the Bering Sea. *Cont. Shelf Res.* **8**:1299–1320.

Zeeman, S.I. (1985) The effects of tropical storm Dennis on coastal phytoplankton. *Estuar. Coast. Shelf Sci.* **20**:403–418.

Zeeman, S. I. (1992) The importance of primary production and CO<sub>2</sub>. In: *Results of the Third Joint U.S.-U.S.S.R. Bering and Chukchi Seas Expedition (BERPAC), Summer 1989*. P.A. Nagel (ed.) Wash. D.C.: U.S. Fish and Wildlife Serv., pp. 218–224.

Zeeman, S.I., and Jensen, P.R. (1990a) Modeling primary production in the Bering Sea. In: *Results of the Second Joint U.S.-U.S.S.R. Bering Sea Expedition, Summer 1984*. P.F. Roscigno (ed.). U.S. Fish and Wildlife Serv. Biol. Rep. 90(13), pp. 74–86.

Zeeman, S.I., and Jensen, P.R. (1990b) Photoresponses of phytoplankton in the Bering Sea. In: *Results of the Second Joint U.S.-U.S.S.R. Bering Sea Expedition, Summer 1984*. P.F. Roscigno (ed.). U.S. Fish and Wildlife Serv. Biol. Rep. 90(13), pp. 87–96.

Zimmerman, R.C., Cabello-Pasini, A., and Alberte, R.S. (1994) Modeling daily production of aquatic macrophytes from irradiance measurements: A comparative analysis. *Mar. Ecol. Prog. Ser.* **114**:185–196.

**Table 1.** Primary production in the eastern and central Aleutian Passes.

Period	Eastern Passes		Central Passes	
	(mg C m <sup>-2</sup> d <sup>-1</sup> )	(n)	(mg C m <sup>-2</sup> d <sup>-1</sup> )	(n)
June 1968 and 1970	220 ± 270	10	300 ± 140	4
June 2001	3810 ± 360	5	910 ± 150	4
May 2002	2760 ± 240	10	----	--
June 2002	430 ± 90	9	770 ± 70 <sup>a</sup>	16

<sup>a</sup> Including Samalga Pass

**Table 2.** Nutrient transport through the major eastern and central Aleutian Passes in summer.

Pass (sill depth)	Volume	Nitrate		Phosphate		Silicic Acid	
		Transport <sup>a</sup> (10 <sup>6</sup> m <sup>3</sup> s <sup>-1</sup> )	Concentration (μM)	Transport (10 <sup>3</sup> moles s <sup>-1</sup> )	Concentration (μM)	Transport (10 <sup>3</sup> moles s <sup>-1</sup> )	Concentration (μM)
<i>Eastern</i>							
Unimak (52 m)	0.3	6	2	0.3	19	6	
Akutan (30 m)	0.1	10	1	0.1	24	2	
<i>Transition</i>							
Samalga (200 m)	0.4 <sup>b</sup>	18	7	0.7	41	16	
<i>Central</i>							
Amukta (0–200 m) <sup>c</sup>	3	24	71	6	49	146	
Amukta (200–430 m)	1	37	37	3	87	87	
Seguam (165 m)	0.4	27	11	0.9	57	23	
Tanaga (235 m)	0.4 <sup>d</sup>	30	12	1	59	24	
<i>Total<sup>e</sup></i>	5.6		141	12		304	

<sup>a</sup> From Stabeno *et al.*, 2004

<sup>b</sup> Unpublished data

<sup>c</sup> Tidal mixing in Amukta Pass extends to about 200 m.

<sup>d</sup> Volume transport was not measured, but assumed to be similar to Seguam Pass as these passes are similar in size (Ladd *et al.*, 2004).

<sup>e</sup> Assumes that transport through the remaining eastern passes was negligible.

## FIGURES

Figure 1. A map of the study area showing the location of moorings (stars in the GoA and Seguam Pass), hydrographic stations in 2001 (red) and 2002 (green) and historical hydrographic stations from WOCE P14 stations (blue).

Figure 2. Concentration of nitrate ( $\mu\text{M}$ ) through the Aleutian Passes in 2001 (left) and 2002 (right) overlaid with contours of density ( $\sigma_t$ ) at  $0.2 \text{ kg m}^{-3}$  intervals. Arrows identify the location of pertinent production stations numbered sequentially as in the appendix. Dates of production stations and hydrographic sections were not always identical.

Figure 3. Concentration of phosphate ( $\mu\text{M}$ ) through the Aleutian Passes as in Fig. 2.

Figure 4. Concentration of silicic acid ( $\mu\text{M}$ ) through the Aleutian Passes as in Fig. 2.

Figure 5. Plots of nitrate-salinity (a, b), phosphate-salinity (c, d), and silicic acid-salinity (e, f) for all of the hydrographic data (full water column) in 2001 (left) and 2002 (right) along with nitrate-phosphate diagrams (g, h). Black symbols are for deeper stations from Samalga Pass to the west, gray symbols are for shallower stations east of Samalga.

Figure 6. Concentration of chlorophyll ( $\text{mg m}^{-3}$ ) through the Aleutian Passes as in Figure 2.

Figure 7. A composite of SeaWiFS chlorophyll ( $\text{mg m}^{-3}$ ) in summer (August–September) from 1998–2003 (a) along with a map of the number of images per pixel used in the composite (b).

Figure 8. Integrated daily primary production ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) in the Aleutian Passes for June 2001 (top) and May–June 2002 (bottom, inset are the eastern passes in May). Production stations are numbered sequentially for each year as in the appendix.

Figure 9. Longitudinal distribution of integrated daily production for June 2001 (open circles), May 2002 (x) and June 2002 (filled circles). The dashed line indicates the longitude of Samalga Pass.

Figure 10. Timeseries of moored nitrate+nitrite (black), salinity (red), and northward currents (black) at 151 m in southern Seguam Pass in 2001 (top) and 2002 (bottom). Discrete samples (circles) are from four hydrographic stations occupied 18–27 km to the west in 2001 and interpolated to 151 m.

Figure 11. Property-property plots from the 151 m mooring in Seguam Pass; nitrate+nitrite against salinity from 2001 (a) and 2002 (b), and T-S diagrams from 2001 (c) and 2002 (d). For comparison, hydrographic data (x) are also shown in (a) and (b). In the T-S diagrams, the MicroCat data are in black, except for data collected from the MicroCat during the period in which the nutrient monitor was operating (overlaid in gray).

Figure 12. Nitrate-salinity diagram. Spring mooring data in the GoA (dark grey) were from the mouth of Amatuli Trough in 2001 (185 m) and 2002 (192 m), the head of Amatuli Trough in 2002 (161 m), and Chiniak Trough in 2002 (123 m). Seguam Pass moorings in 2001 (green) and 2002 (red) were at 151 m. Data from the 1993 WOCE P14 cruise (blue) include hydrographic stations 13–25 from 50–500 m.

**Appendix.** Photosynthesis — irradiance parameters and primary production from sequentially numbered production stations.

Sta.	Date	Island/Pass	Latitude	Longitude	Depth	Alpha	P <sub>max</sub>	Primary Production
					(m)	$\frac{(\text{mg C mg chl}^{-1} \text{ hr}^{-1})}{(\mu\text{mol photon m}^{-2} \text{ s}^{-1})}$	$(\text{mg C mg chl}^{-1} \text{ hr}^{-1})$	$(\text{mg C m}^{-2} \text{ d}^{-1})$
<b>2001</b>								
1	June 1	Krenitzin Is.	54.05	164.86	5	0.122 ± 0.017	9.2 ± 4.6	3,280 ± 471
					37	0.124 ± 0.048	15.0 ± 7.5	
2	June 8	Umnak Is.	52.92	168.45	0	0.014 ± 0.002	1.0 ± 0.5	1,838 ± 203
					30	0.022 ± 0.004	1.1 ± 0.5	
3	June 10	Seguam P.	52.36	172.99	0	0.026 ± 0.004	1.7 ± 0.8	980 ± 121
					30	0.032 ± 0.004	1.3 ± 0.7	
4	June 11	Seguam P.	51.99	172.50	0	0.018 ± 0.003	1.2 ± 0.6	485 ± 74
					30	0.011 ± 0.004	0.7 ± 0.4	

5	June 12	Amukta P.	52.61	171.84	0	0.025 ± 0.003	1.3 ± 0.6	432 ± 56
					25	0.029 ± 0.006	1.2 ± 0.6	
6	June 13	Amukta P.	52.17	171.74	0	0.040 ± 0.009	4.6 ± 2.3	1,759 ± 429
					15	0.029 ± 0.005	2.1 ± 1.1	
7	June 14	Akutan P.	54.13	166.44	15	0.083 ± 0.009	5.0 ± 2.5	6,810 ± 922
					38	0.034 ± 0.005	1.2 ± 0.6	
8	June 18	Unimak P.	54.56	165.80	0	0.034 ± 0.004	3.1 ± 1.5	6,373 ± 961
					30	0.063 ± 0.011	3.1 ± 1.6	
9	June 20	Unimak P.	54.18	164.41	0	0.015 ± 0.003	1.3 ± 0.6	733 ± 142
					45	0.025 ± 0.006	0.7 ± 0.4	
<b>2002</b>								
1	May 20	Unimak P.	54.20	165.66	0	0.030 ± 0.006	3.3 ± 0.2	4,474 ± 1,047
					50	0.009 ± 0.001	1.0 ± 0.1	
2	May 20	Unimak P.	54.35	165.04	0	0.034 ± 0.006	2.0 ± 0.1	2,243 ± 544
					30	0.025 ± 0.005	1.6 ± 0.1	

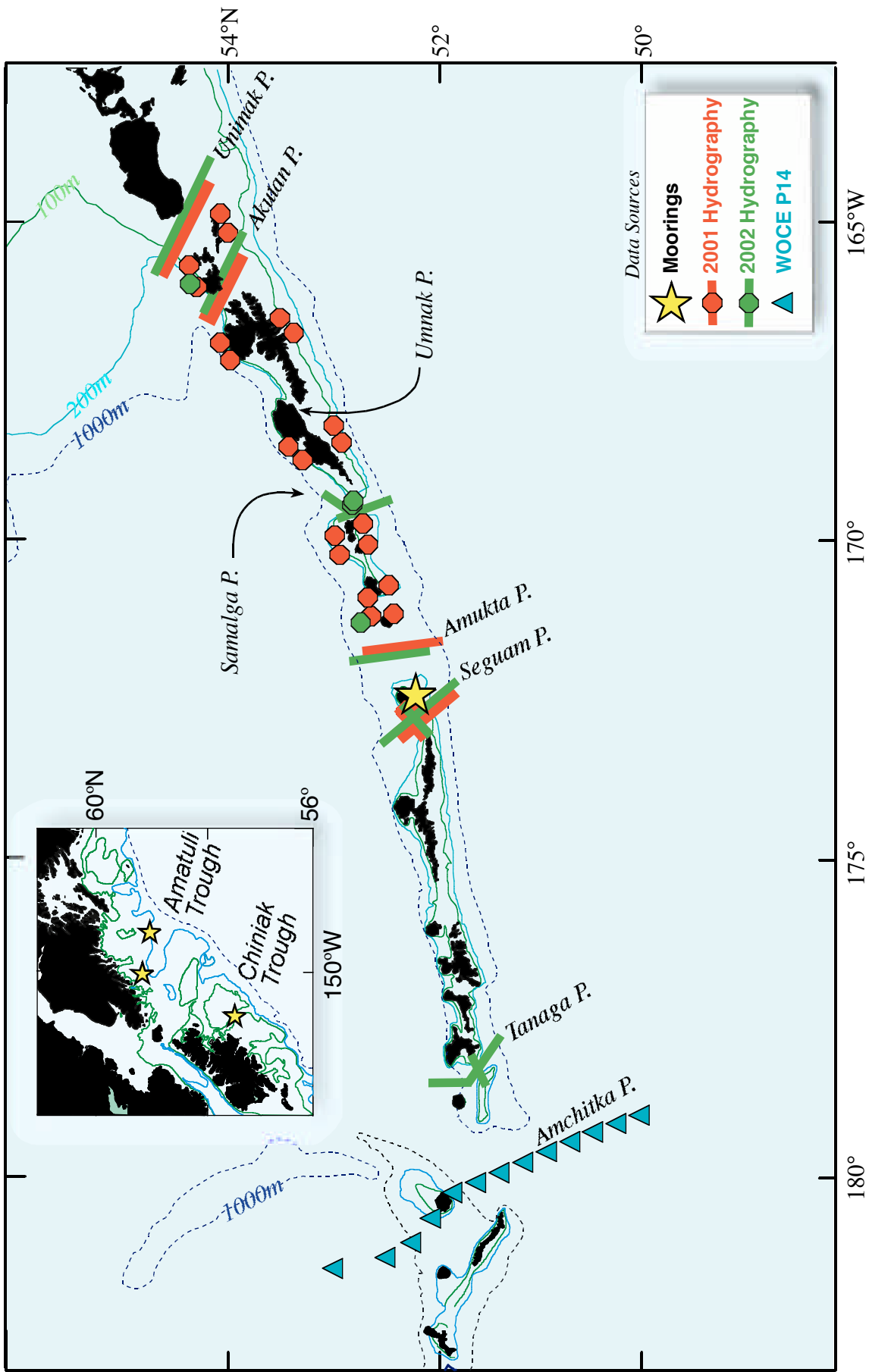


3	May 21	Akutan P.	54.10	166.17	0	0.005 ± 0.002	0.3 ± 0.0	212 ± 63
4	May 22	Akutan P.	54.15	166.51	0	0.013 ± 0.002	1.6 ± 0.1	2,084 ± 332
					45	0.016 ± 0.004	1.8 ± 0.1	
5	May 22	Akutan P.	54.10	166.17	0	0.013 ± 0.003	1.3 ± 0.1	536 ± 74
					20	0.017 ± 0.003	1.5 ± 0.1	
6	May 22	Akutan P.	53.86	165.47	0	0.039 ± 0.007	2.7 ± 0.2	3,506 ± 1,148
					20	0.028 ± 0.007	2.2 ± 0.2	
7	May 24	Akutan P.	54.15	166.51	0	0.010 ± 0.001	1.0 ± 0.0	6,574 ± 845
					12	0.010 ± 0.003	1.0 ± 0.1	
8	May 25	Unimak P.	54.20	165.66	0	0.022 ± 0.003	1.9 ± 0.1	1,142 ± 155
					30	0.021 ± 0.003	1.3 ± 0.1	
9	May 25	Unimak P.	54.33	164.96	0	0.020 ± 0.003	1.4 ± 0.1	3,246 ± 1,027
					10	0.010 ± 0.008	1.5 ± 0.4	
10	May 25	Unimak P.	54.08	164.06	0	0.042 ± 0.005	2.3 ± 0.1	3,561 ± 365
11	May 29	Tanaga P.	51.68	178.41	0	0.012 ± 0.008	2.2 ± 0.6	208 ± 216
12	May 29	Tanaga P.	51.43	177.74	0	0.012 ± 0.001	1.9 ± 0.1	242 ± 20

13	May 30	Tanaga P.	52.07	178.48	0	40	0.024 ± 0.009	0.9 ± 0.1	
14	May 30	Tanaga P.	51.68	178.41	0		0.011 ± 0.006	1.6 ± 0.3	124 ± 60
15	June 2	Seguam P.	52.45	173.12	0		0.011 ± 0.003	2.2 ± 0.2	337 ± 78
					35		0.017 ± 0.007	2.4 ± 0.4	1,974 ± 310
							0.023 ± 0.010	1.5 ± 0.2	
16	June 2	Seguam P.	52.21	172.80	0		0.019 ± 0.004	2.1 ± 0.2	2,078 ± 208
17	June 3	Seguam P.	52.45	173.13	0		0.019 ± 0.009	2.2 ± 0.4	1,309 ± 476
					35		0.024 ± 0.015	1.8 ± 0.3	
18	June 3	Seguam P.	51.87	172.33	20		0.007 ± 0.009	1.8 ± 1.0	202 ± 261
19	June 4	Seguam P.	52.28	172.89	16		0.018 ± 0.008	2.4 ± 0.4	1,526 ± 332
20	June 4	Seguam P.	52.28	172.89	10		0.009 ± 0.001	1.4 ± 0.1	2,478 ± 461
21	June 5	Amukta P.	52.49	171.80	0		0.009 ± 0.004	2.1 ± 0.4	87 ± 42
					35		0.012 ± 0.004	1.9 ± 0.2	
22	June 5	Amukta P.	52.73	171.87	20		0.046 ± 0.060	3.3 ± 1.4	337 ± 269
23	June 6	Amukta P.	52.18	171.73	20		0.019 ± 0.003	2.2 ± 0.1	288 ± 23
24	June 7	Samalga P.	53.09	169.28	25		0.028 ± 0.010	2.4 ± 0.3	273 ± 61

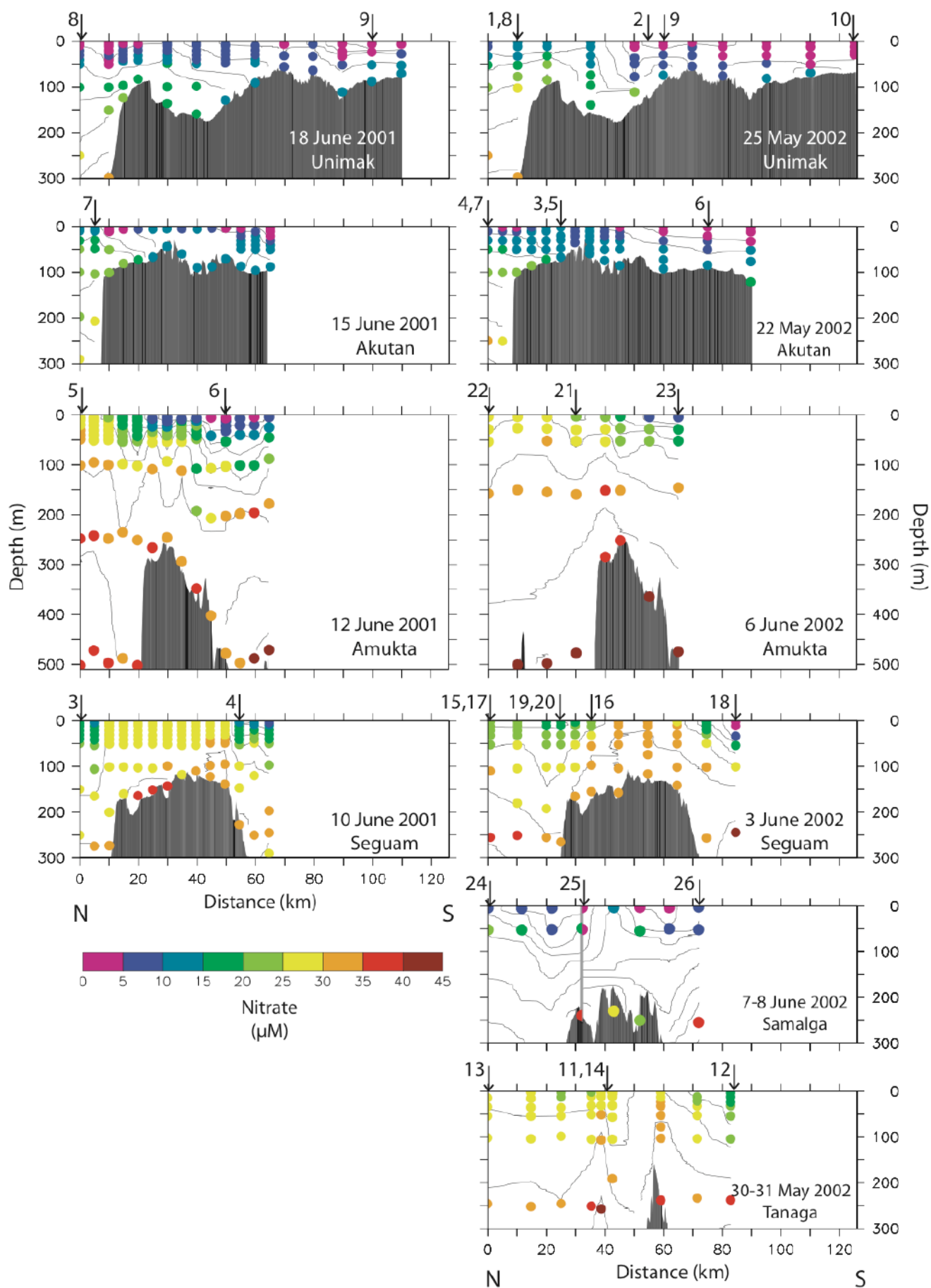
25	June 7	Samalga P.	52.80	169.47	15	0.016 ± 0.018	1.4 ± 0.5	406 ± 376
26	June 8	Samalga P.	52.47	169.36	0	0.009 ± 0.002	0.9 ± 0.1	409 ± 93
27	June 10	Umnak P.	53.64	167.68	0	0.007 ± 0.005	1.1 ± 0.3	40 ± 28
28	June 10	Umnak P.	53.39	167.76	15	0.002 ± 0.003	0.5 ± 0.3	164 ± 49
29	June 10	Umnak P.	53.12	167.93	20	0.005 ± 0.007	0.6 ± 0.3	94 ± 82
30	June 12	Unimak P.	54.50	165.59	0	0.005 ± 0.005	1.0 ± 0.4	601 ± 245
31	June 12	Unimak P.	54.27	164.75	15	0.006 ± 0.001	1.1 ± 0.1	213 ± 42
32	June 12	Unimak P.	54.10	164.13	25	0.010 ± 0.002	0.8 ± 0.0	274 ± 27
33	June 15	Akutan P.	54.15	166.51	0	0.015 ± 0.003	2.2 ± 0.1	822 ± 276
34	June 15	Akutan P.	54.04	166.10	0	0.015 ± 0.005	1.7 ± 0.2	511 ± 87
35	June 16	Akutan P.	53.81	165.27	0	0.032 ± 0.015	3.3 ± 0.6	1,117 ± 549

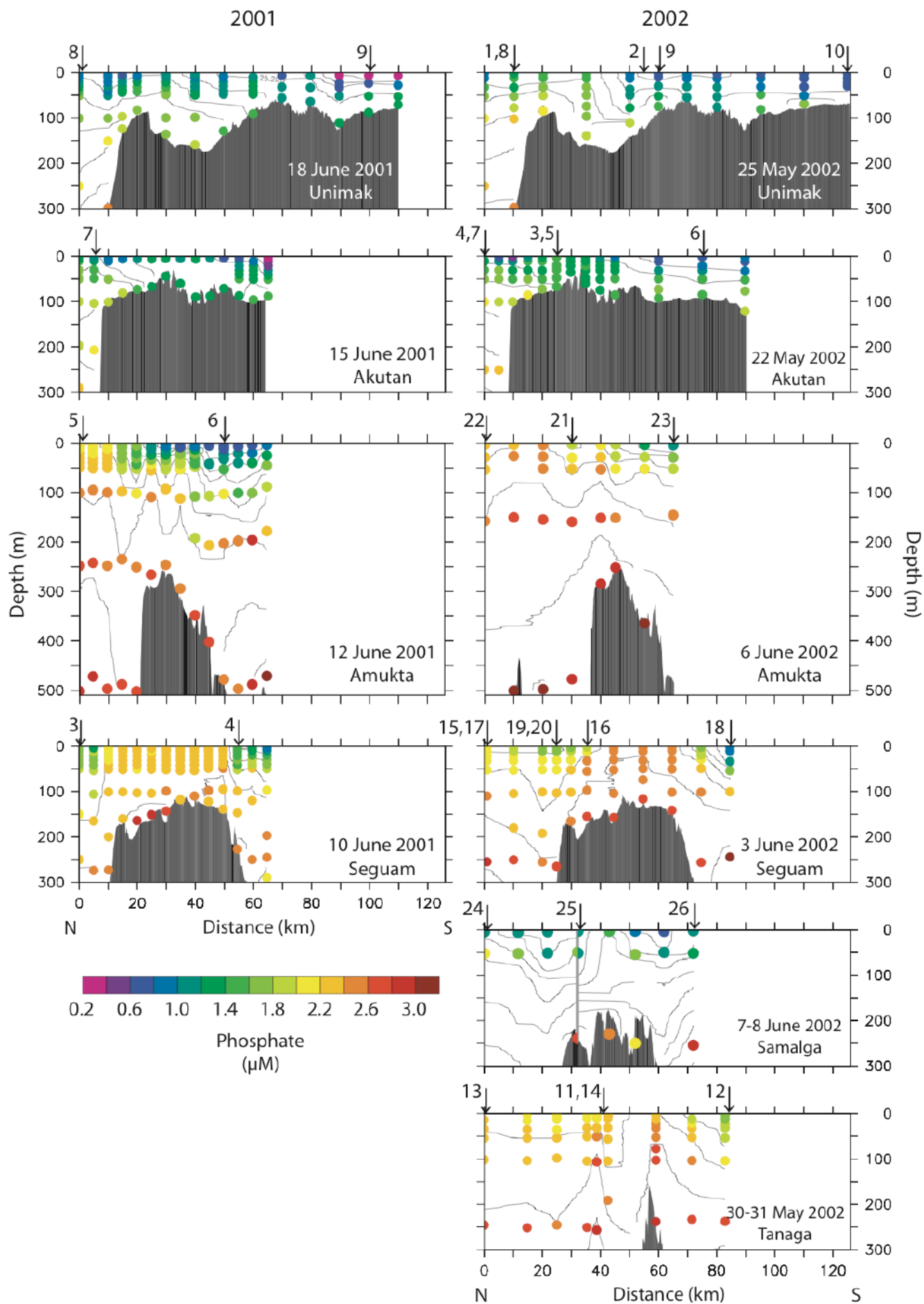
---



2001

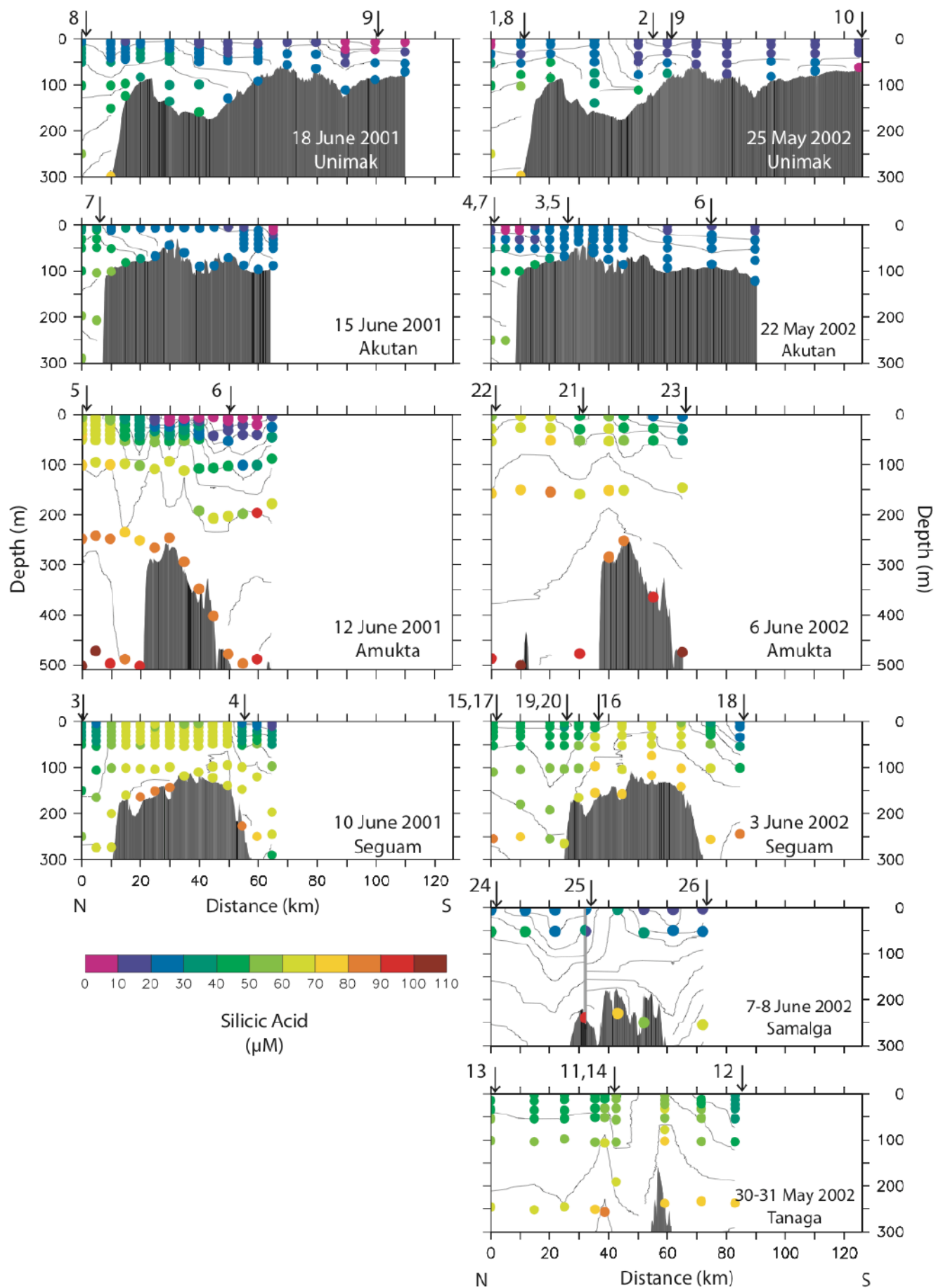
2002



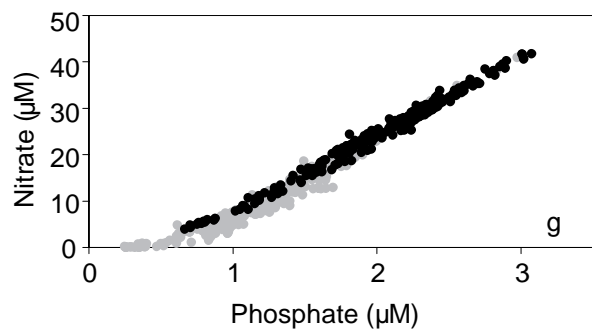
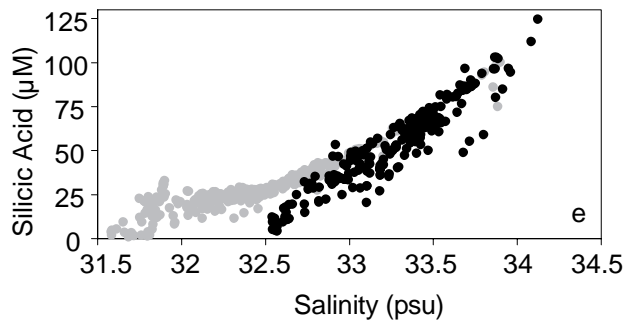
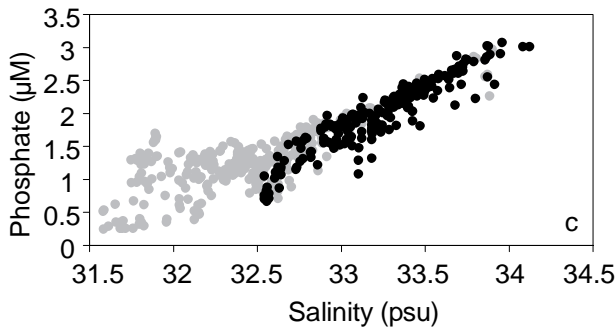
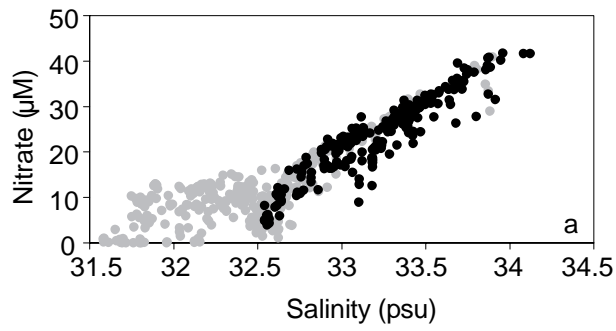


2001

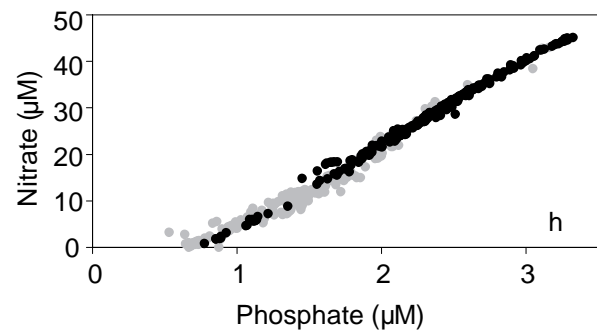
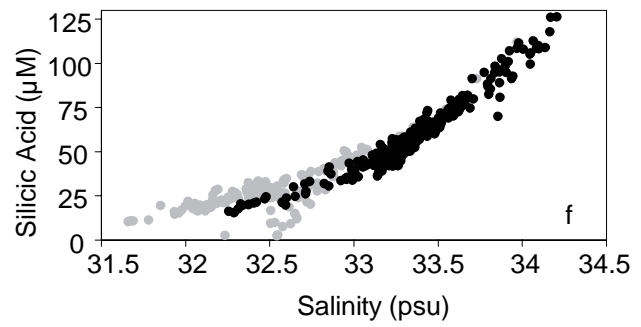
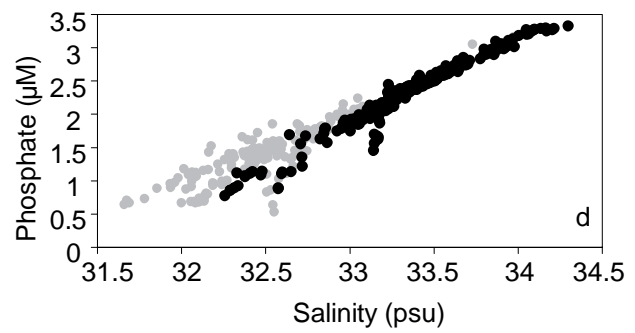
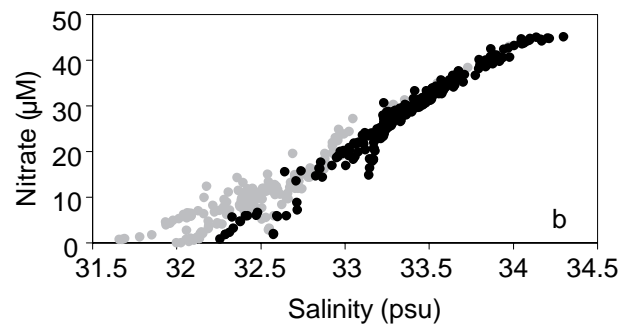
2002



2001



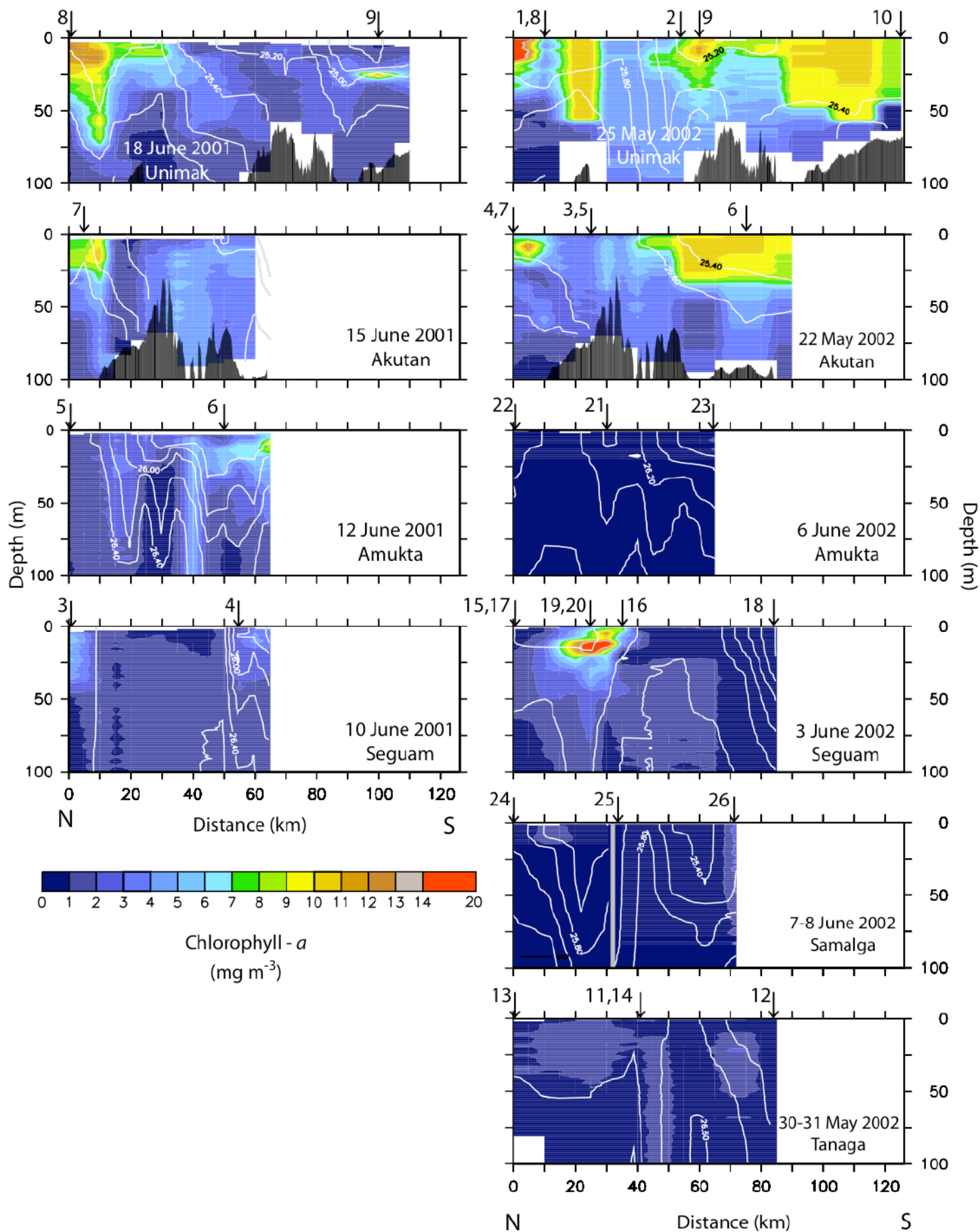
2002

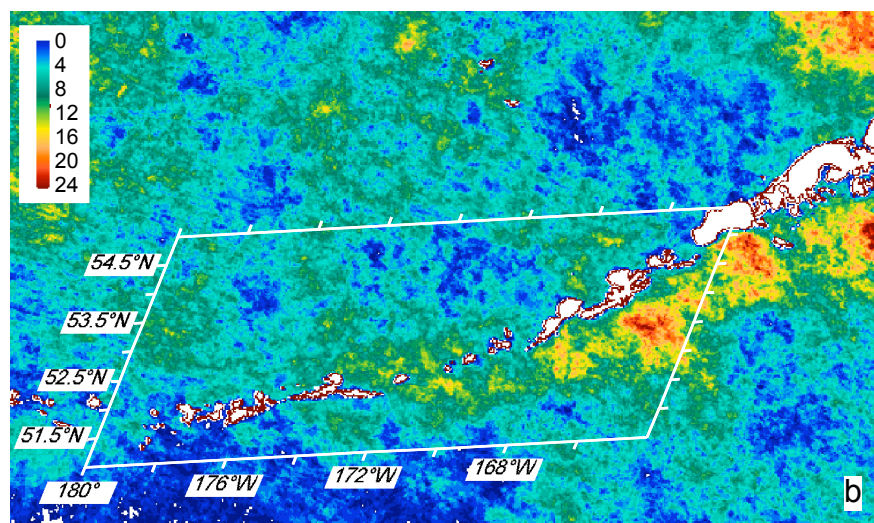
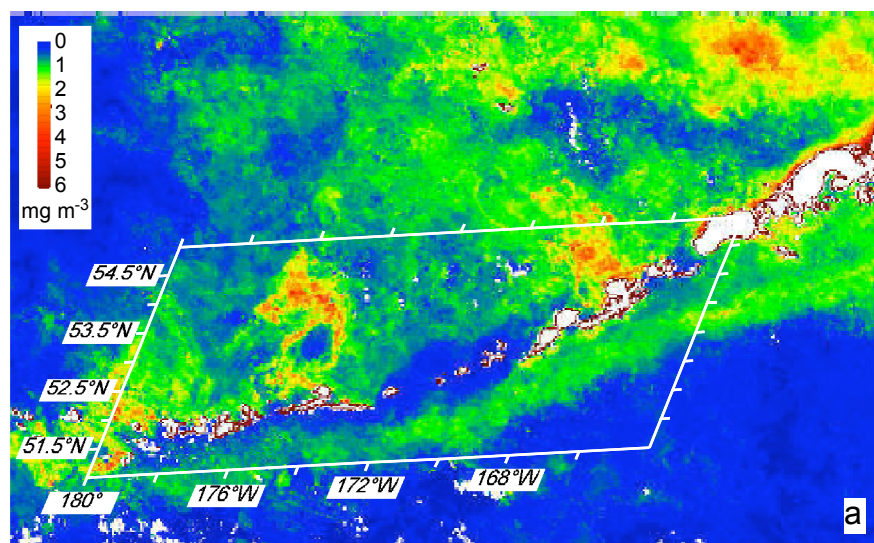


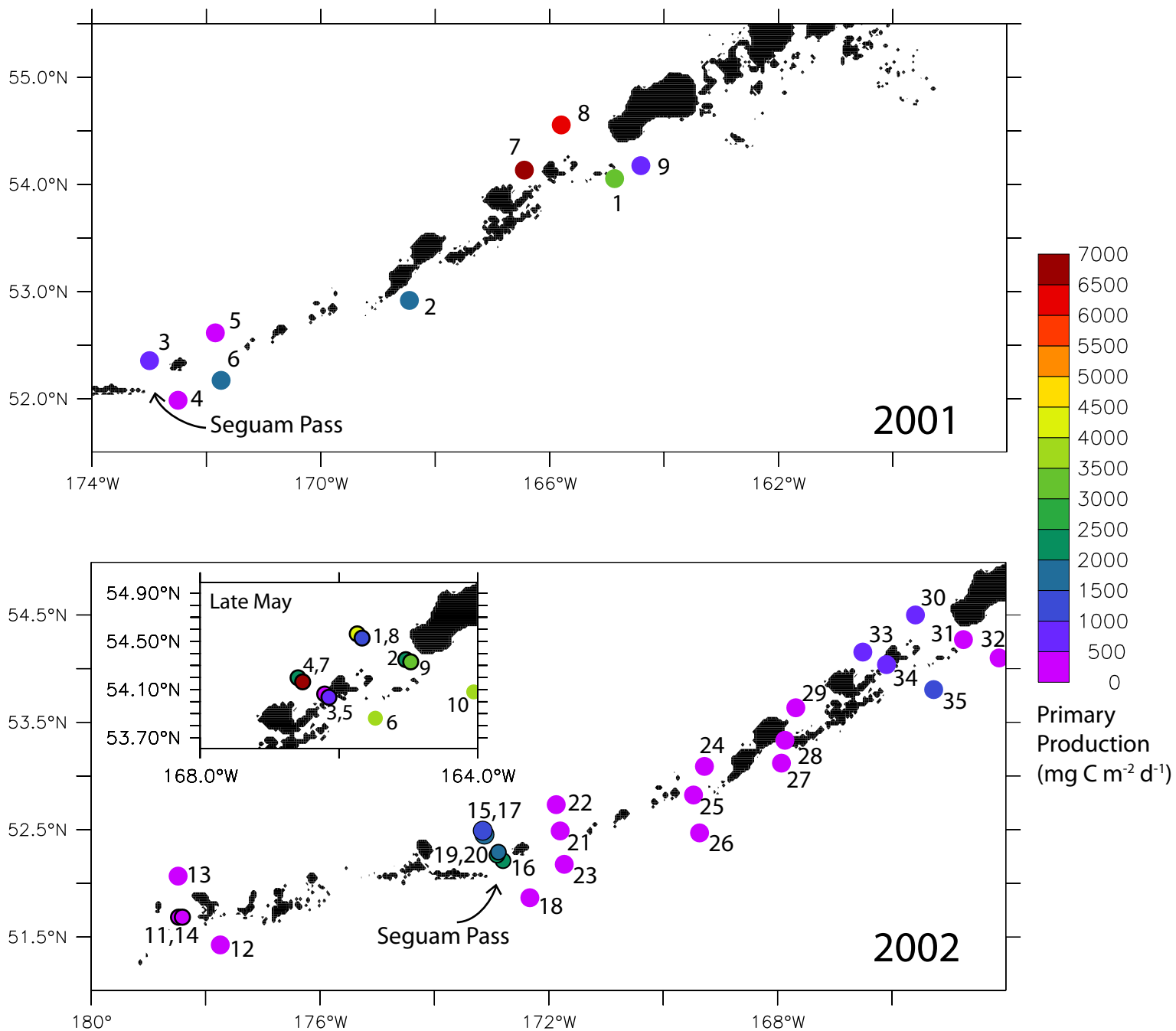


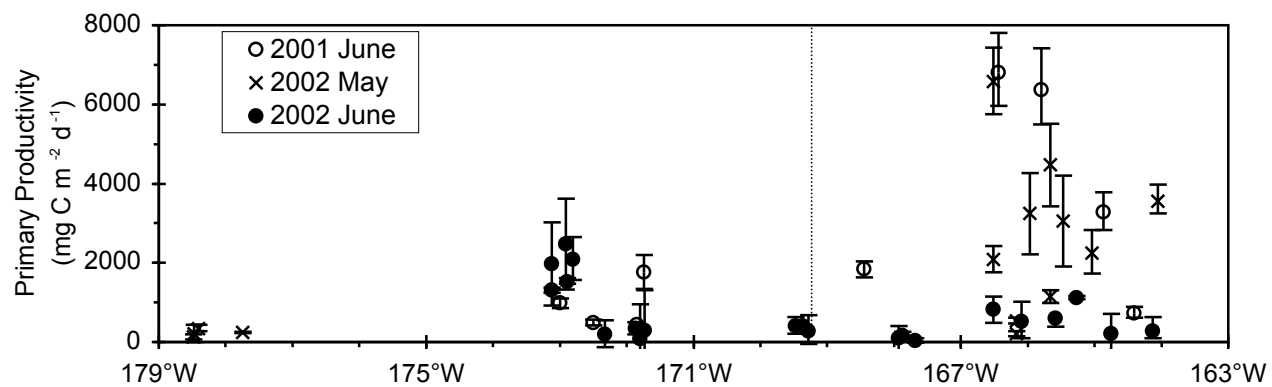
2001

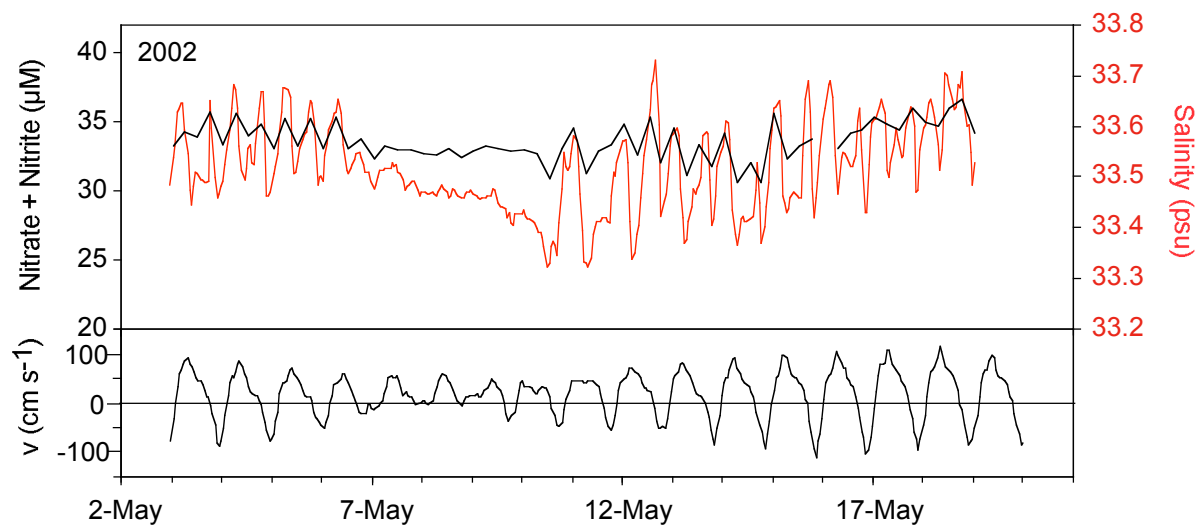
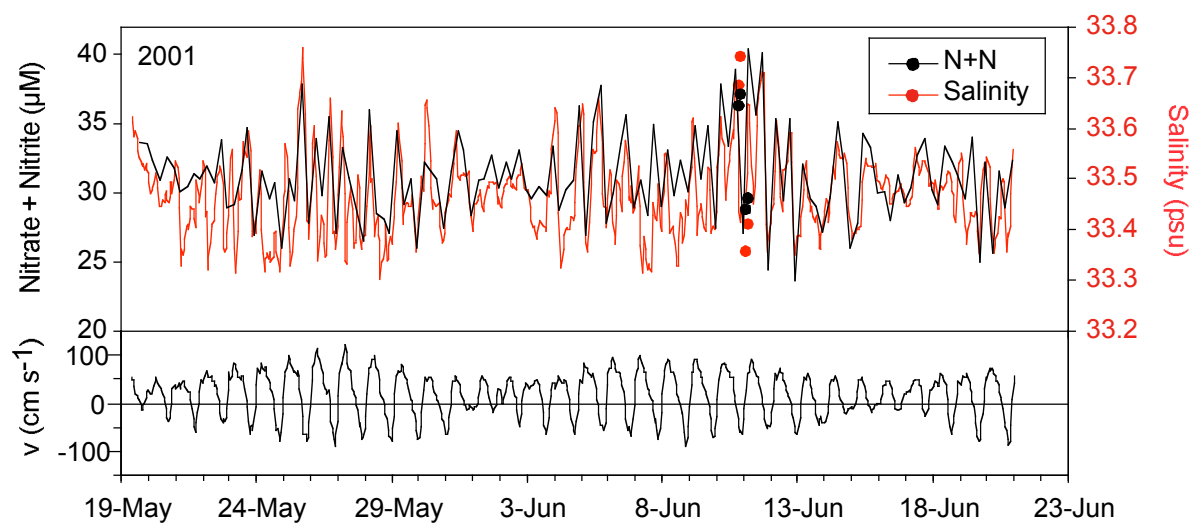
2002



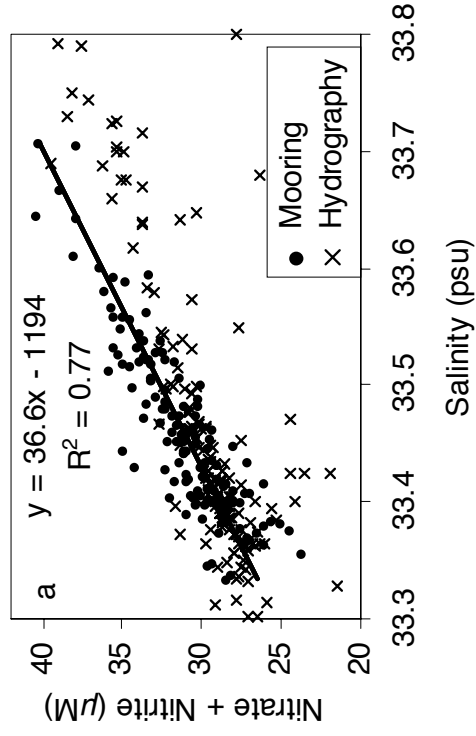








2001



2002

